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Apparent selective advantage of leucism in a coastal population of Southern caracaras (Falconidae)

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ABSTRACT

Background: Southern caracaras are medium-sized raptors with a large range stretching to the southern tip of South America. An aberrant, leucistic plumage is found commonly along the coast of Chubut Province (Patagonia, Argentina). Leucistic birds do not produce dark melanin in their feathers. However, they are not albinos because their eyes are not red. No genetic studies of caracara plumages are known.

Hypothesis: The high frequency of leucistic birds in Chubut Province arises because of natural selection.

Methods: Map the distribution of leucistic individuals relative to normal individuals. Combine a variety of anecdotal natural history observations, collected over 20 years, into a logical inference.

Observations: Leucistic caracaras were found only along a 250-km stretch of rocky oceanic islands and continental outcrops with large seabird colonies in Chubut Province. In the rest of their range, Southern caracaras have dark plumage. Where they do occur, leucistic birds are frequent and co-occur with dark-plumaged birds. Intermediate individuals, presumably

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heterozygotes, exist. Leucism is not related to age or sex. Leucistic individuals are restricted to a particular habitat. Gene flow has not homogenized the coastal and inland populations.

Results: Leucism is not simply due to inbreeding producing more homozygous individuals. Leucism is not due to genetic drift. Leucism is not an environmental effect on individual physiology or development. Leucism is not a transient (plastic) phenomenon. Where they occur frequently, leucistic Southern caracaras are apparently favoured by natural selection, either directly or by pleiotropy.

Keywords: albinism, *Caracara plancus*, colour, inbreeding, leucism, polymorphism, selection.

INTRODUCTION

Many species of raptor as well as other birds show a great variability in colour. This variability can occur as continuous variation between paler and darker extremes, or as distinct pale and dark morphs (reviewed in Roulin, 2004). The ultimate explanation for such existence and maintenance of colour polymorphism remains elusive. Several hypotheses have been advanced to explain polymorphism in birds, such as apostatic selection due to prey image-avoidance, disruptive selection stemming from ecological specialization, thermoregulation, imprinting, and sexual or social selection. However, the support for none of them is particularly strong (see Galeotti *et al.*, 2003; Fowlie and Krüger, 2004; Galeotti and Rubolini, 2004; Roulin, 2004; Roulin and Wink, 2004; Gray and McKinnon, 2006).

Here we describe and interpret the existence of an unusual population of Southern caracaras *Caracara plancus* with a high frequency of pale individuals. Southern caracaras normally have an overall dark-brown plumage (see Fig. 1). The species has a large and continuous range that stretches from Amazonia to the southern tip of South America (Dove and Banks, 1999). They inhabit a variety of open and half-open habitats. Given the exclusive presence of dark-plumaged birds over most of South America, the existence of a population with a high frequency of aberrant pale-plumaged individuals is highly intriguing and begs an explanation. We therefore evaluated a number of alternative hypotheses that might explain this phenomenon.

METHODS

Our study area comprises the Argentinean part of Patagonia, South America. Partly due to its remoteness and difficulty of access, we have not performed a specific study on leucistic caracaras. However, over the past two decades we have been involved in other studies on both the mainland and the coastal areas where Southern caracaras regularly occur. By compiling all observations of caracaras, we constructed a map of the distribution of pale and normal individuals. In addition, we studied 57 images from four pale museum specimens, and 60 images from at least ten different pale individuals in the field (see Fig. 1) to extract information on the pale plumage.

The non-quantitative nature of our information precludes the valid use of statistics to infer patterns and test hypotheses. Instead, we combined the information on distribution and plumage in the light of the biology of the species. With this, we evaluated a number of alternative explanations for the local high frequency of pale-plumaged birds: (1) an environmental effect, (2) inbreeding, (3) genetic drift, or (4) natural selection.

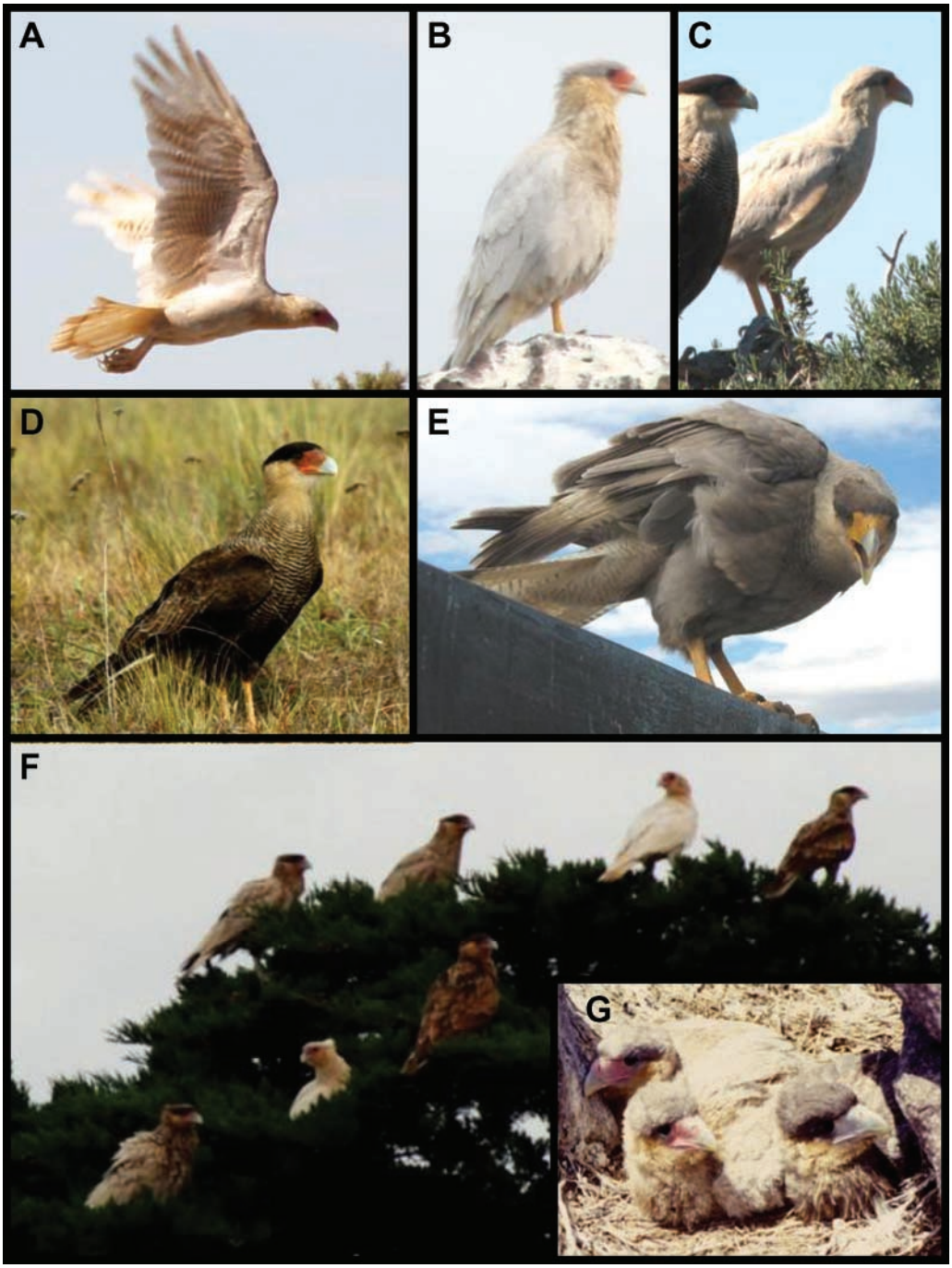

Fig. 1. Overview of colour variation as encountered in Southern caracaras along the coast of Chubut Province, Argentina. (A, B) white morph, (C) white morph paired with normal dark individual, (D) normal dark individual, (E) intermediate bird, (F) mixed flock consisting of two white morph individuals, three intermediate individuals, and two normal dark (but bleached and worn) immature individuals (top row and bottom row rightmost individuals), (G) brood with two white and one intermediate chick (rightmost).

RESULTS

Description of pale Southern caracaras

The overall colour of the palest birds ('white morphs') is white with a greyish or brownish cast (Fig. 1). Upon closer inspection of the barring pattern of individual feathers, it appears that dark melanins are missing or highly reduced, but that brownish to yellowish colours are unaffected or even more strongly expressed compared with normal, dark-coloured birds. Thus, the plumage is mostly white in those parts that are normally brownish-black, and remaining colour is mostly found in those parts that are normally palest. This creates a highly aberrant, almost 'negative-image' impression. Bare parts seem unchanged: a pale blue bill with reddish-pink cere, yellowish legs, and dark eyes. The absence of red eyes indicates that these pale birds should not be called albinistic (i.e. unable to produce melanin at all) but leucistic (Harrison, 1985).

Interestingly, intermediate individuals are also present (Fig. 1). Based on 30 images of six such individuals (both perched and flying), intermediates show a grey (not normal brown to black) overall plumage, with a darker brown cap and often the same brownish-yellow cheeks and throat as the white morph. The wings are also grey, but with reduced pigmentation in the tips of primaries and secondaries. Some individuals were rather blotchy. This effect seems to be due to the presence of bleached, older feathers and darker, newer feathers (as often seen in larger raptors).

As in normal coloured individuals, immature leucistic birds can be distinguished from adults by brownish vertical streaks (not horizontal barring) on the upper chest (Fig. 1). In the white morph, these can be very pale and difficult to see in the field.

Distribution, habitat, and population size

We found this particular kind of leucistic caracara only along the southern coast of Chubut Province, Argentina (see Fig. 2). Additional anecdotal observations of leucistic caracaras from the same area go back over 100 years (Durnford, 1878; Bó, 1958). Leucistic caracaras seem almost entirely restricted to a number of small islands within about 20 km of the coast, and to rocky coastal outcrops along the continent. The southernmost records are from Bahía Bustamante (45°16′S, 66°50′W), and the northernmost record is from Punta Tombo (44°03′S, 65°20′W). The distribution of leucistic caracaras covers about 250 km of coastline, so the occurrence of leucistic caracaras is not a small-scale phenomenon.

The distribution of leucism coincides with the limits of volcanic siliceous red rocks of the Marifil formation (Del Valle, 1998) along the Chubut coast, which forms the majority of islands and outcrops. These relatively hard rocks are poorly vegetated and have low abundances of mammalian prey species (personal observation). However, the islands and rocky outcrops are home to large seabird colonies, regularly consisting of thousands to tens of thousands of breeding pairs of penguins, cormorants, gulls, and terns (Yorio *et al.*, 1998). These seabird colonies and other, intermittent stretches of coastline have been studied over the years with a varying degree of intensity in studies unrelated to caracaras. Yet pale caracaras have never been seen more than a few hundred metres away from such seabird concentrations. Thus they may be said to be exclusive to the coastal zone in general and to places with high densities of seabirds in particular. On the other hand, normal dark-coloured individuals are found virtually across the entire South American continent. Normal birds have also been

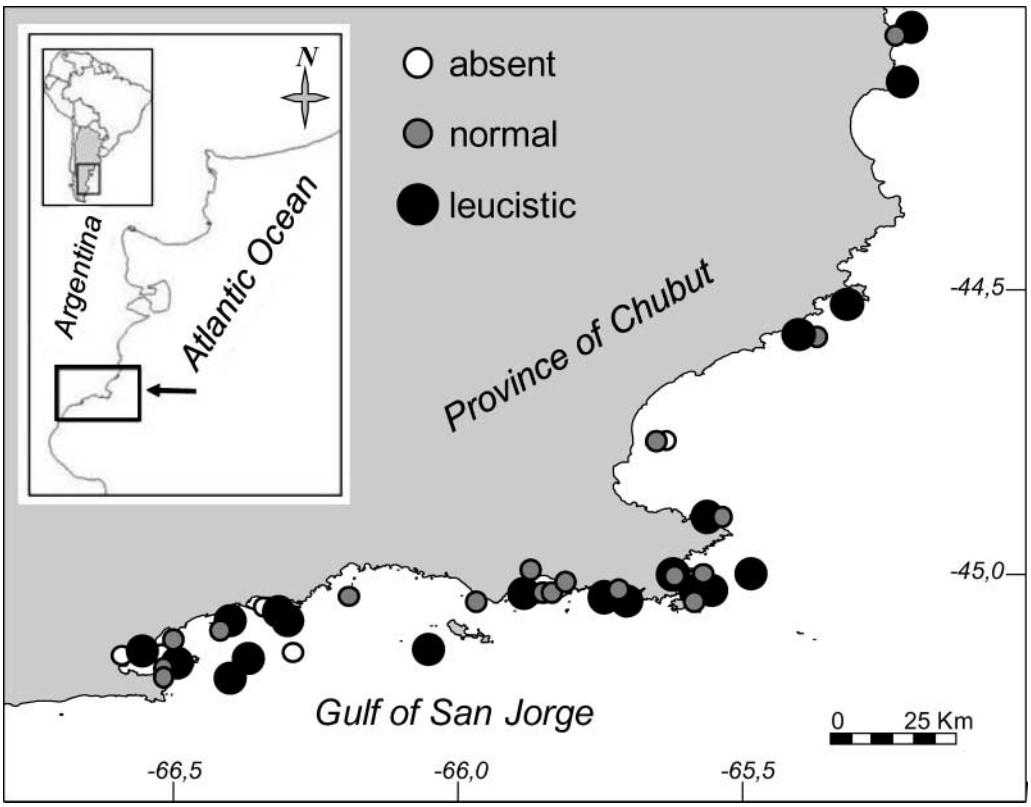

Fig. 2. Overview of observations of normal-coloured and leucistic (white morph or intermediate) Southern caracaras along the coast of Chubut Province, Argentina. Also plotted are sites were no caracaras were observed during a visit.

encountered in these coastal habitats, especially in or close to seabird colonies on the continent but even on some of the islands. Hence, the distribution of normal and leucistic individuals overlaps partially (Fig. 2).

Without any formal census data, we can give only a very crude estimate of the population size of the white morph. Observations of white individuals in different locations could conceivably be related to the same individual. We feel that this is mostly not the case. Extreme territorial site-faithfulness has been reported for adults of the formerly conspecific Northern caracara *Caracara cheriway* (Morrison, 1999). A white morph individual was continuously present at Punta Tombo for seven consecutive years, suggesting the same is true in our population. In view of our data and the limited number of suitable islands and rocky outcrops along the coast, the total population most likely consists of fewer than a hundred individuals.

Clues to sex- or age-linkage and the genetic basis of the leucistic plumage

If we want to infer the ultimate mechanism responsible for the occurrence of this habitat-restricted population of leucistic individuals, then information on the ontogeny and

potential genetic basis of the leucistic plumage is necessary. The following observations are relevant with respect to sex- or age-linkage and the genetic basis of the leucistic plumage. First, there are several records of white morph breeding pairs with white morph chicks in the nest. One breeding pair of a white morph and an intermediate individual produced a brood with two white morphs and one intermediate offspring (Fig. 2). Second, the museum specimens include a fledged juvenile and an adult male and female (sexed on gonads). Third, one intermediate individual was closely associated with a white individual during the breeding season and the two seemed to be paired, suggesting that both birds had attained adult plumage. In addition, both birds had just started primary moult, and the newly grown, innermost primaries were only slightly darker than the older feathers. Fourth, it seems that the variation in plumage colour can be classified into three groups: white morph, intermediate, or normal. However, one does see individual variation within these classes, for example, white morph birds with more or less brown barring.

DISCUSSION

We observed white morph individuals of all sexes and ages, including chicks in the nest. The lack of colour change in the moulting adult white morph and intermediate individuals supports the conclusion that both white morph and intermediate birds do not change colour with age, other than because of normal bleaching of feathers. These observations show that the white morph is not strictly sex- or age-limited. The colour variation of the coastal caracaras seems to consist of three discrete classes: white morph birds, intermediate birds, and normal dark birds. Although our sample size is extremely limited, we never observed normal-coloured offspring in the broods of pale-coloured parents. A cross between a white and an intermediate individual produced two white and one intermediate offspring. This, and the impression that intermediate birds are more rare than the white morph, suggests a genetic basis to the leucism that consists of a single mutational step of large effect, and not of many mutations of small effect. The intermediate birds are then interpreted to be heterozygous for a leucism allele. Such single-step mutations are a common phenomenon in avian colour polymorphism (Roulin, 2004). A candidate gene causing such loss of dark pigmentation could be the MC1R locus, since this gene does cause polymorphism in a range of other birds (Mundy *et al.*, 2004). Also, low MC1R activity generally leads to increased synthesis of yellowish or reddish phaeomelanin (Mundy, 2005), which would explain the apparently stronger golden to brownish colours in the white morph caracaras.

One alternative explanation for the occurrence of the leucistic plumage is that it is not heritable but caused by the environment (e.g. by nutritional deficiency), but such cases are rare in the wild (Harrison, 1985; Roulin, 2004). The melanin pigments that produce the dark feathers of normal-coloured caracaras are synthesized by the birds themselves and do not depend on nutrient uptake from the environment (as is the case for carotenoids, for example). Yet there is some evidence that access to certain minerals or trace elements can influence the degree of melanization (McGraw, 2003; Roulin *et al.*, 2006). However, it is unlikely that the particular kind of rock inhabited by these leucistic caracaras disturbs the normal production of melanin, since in the absence of much terrestrial prey on the islands they must mostly depend on food that is produced by the marine environment. This is supported by observed food items: Kelp gull *Larus dominicanus* ($n = 18$), Magellanic penguin *Spheniscus magellanicus* ($n = 15$), Imperial cormorant *Phalacrocorax atriceps* ($n = 2$), Skua *Stercorarius* spp. ($n = 1$), eggs of Chubut flightless steamerduck *Tachyeres leucocephalus* ($n = 2$), and eggs

of Kelp gull ($n = 1$). These food items all have a marine origin. Caracaras feeding on marine resources elsewhere along the coast of South America do not show leucistic plumage (Dove and Banks, 1999), so marine food does not cause the leucistic plumage, at least not directly. In addition, we know of no studies showing how a large proportion of a population exibits leucism due to environmental effects. We therefore reject the hypothesis that leucism in our population is caused by purely environmental effects. Based on the combined evidence, we infer that the leucistic plumages have a genetic basis.

Leucism (often referred to as partial albinism) and albinism are widely reported for hundreds of bird species and can probably be found in any species, given a large enough sample size [e.g. 1 of 146,000 Chinstrap penguins *Pygoscelis antarcticus* (Forrest and Naveen, 2000)]. However, it is very rare to encounter a population with a high frequency of leucistic individuals, and even rarer to see it associated with a particular habitat. Colour polymorphism in other species sometimes also shows geographic variation, but the spatial scale over which such clines are found is often on the order of hundreds or even thousands of kilometres, and may still only affect the relative proportions of each colour morph at the ends of the cline (Roulin, 2004; Antoniazza *et al.*, 2010). In this particular case, the white morph is apparently absent from virtually the entire South American continent (e.g. Dove and Banks, 1999) (but note that there are odd reports of aberrant single individuals, as expected for any common species). In contrast, its regular occurrence is restricted to a long narrow strip of particular coastal habitat where it abruptly reaches a high frequency (Fig. 2). This pattern suggests that its origin and/or maintenance must also have a strong spatial component.

Could local inbreeding explain the high frequency of leucistic caracaras? It is normally believed that leucistic individuals have a reduced fitness, perhaps because of higher predation risk or because of pleiotropic effects on other physiological functions (e.g. Harrison, 1985; Ellegren *et al.*, 1997). Thus, the very rare occurrence of leucistic individuals is normally due to the mating of two heterozygous, normal-coloured individuals each carrying a rare, recessive leucism allele. The frequency of such leucistic individuals in the population would thus depend on a mutation–selection balance, where selection would be incapable of removing all deleterious alleles from the entire population because these alleles are not expressed in heterozygotes (Futuyma, 1998). Since caracaras are relatively common among coastal seabird colonies but less common on the nearby mainland (Carrete *et al.*, 2009; personal observation), it is possible that the degree of inbreeding is higher than normal in the coastal birds. However, under the assumption of selection against leucism, inbreeding could only explain the occurrence of the odd leucistic individual. It cannot explain the high frequency of leucistic individuals in a population, because that calls for a high frequency of alleles causing leucism prior to inbreeding.

Such a necessary increase in the frequency of a rare leucism allele could be caused by stochasticity (genetic drift) if selection is weak (Futuyma, 1998). Therefore, leucism would tend to be observed more in bottlenecked populations (e.g. Bensch *et al.*, 2000; Owen and Shimmings, 1992). One might hypothesize that genetic drift is a sufficient explanation for the high frequency of leucistic individuals. However, the coastal population seems by no means very isolated, and migration reduces the importance of drift (Hartl and Clark, 1997; Futuyma, 1998). Caracaras are found throughout Patagonia, and have a contiguous distribution that includes all coastal areas. In addition, we inferred above that the leucism allele is co-dominant such that heterozygotes are phenotypically distinguishable. This means that the effect of the leucism allele is already exposed to selection in all heterozygote individuals that carry it. That should make selection against leucism many orders of magnitude stronger (to the extent

that heterozygotes have a reduced fitness). This is because an initially rare allele is almost exclusively found in heterozygotes (Hartl and Clark, 1997). For example, if the frequency p of the leucism allele is 0.001 and the frequency of the normal allele $q = 1 - p$, we expect on average 1998 heterozygotes for every single homozygote ($2pq/p^2$). When an allele is under negative selection and already expressed in heterozygotes, this enhanced selection against it makes it much less likely to increase in frequency by genetic drift alone (Hartl and Clark, 1997). Any gene flow from the non-leucistic continental population further reduces the probability that leucism increased due to genetic drift. From this we conclude that the polymorphism in the leucism allele in coastal caracaras is not explained by a mutation–drift–selection balance with selection acting against leucism, but instead by a migration–selection balance with selection favouring leucism. Note that if the leucism does have a polygenic basis, characterized by a more continuous plumage variation from white to normal dark, this does not affect the conclusion that it is improbable that genetic drift or inbreeding resulted in a high frequency of leucistic individuals in the population when selection acts against leucism. Additional data on heritability, amount of interbreeding, neutral genetic differentiation, and movements of white and normal colour morphs could help to ascertain the evolutionary origin and status of the colour morphs.

Is there any scenario for a selective advantage for leucistic caracaras? The white morph is almost exclusively associated with a particular type of habitat, the large seabird colonies found on coastal rocky outcrops and islands. In addition, the range of the morph stretches for about 250 km along the coast, and islands or outcrops are often further apart from each other than from mainland habitat (Fig. 2). This suggests that dispersing white individuals are very selective in which habitat they will set up territories, or that settlement success is very low in the alternative regular mainland habitats. Either way, it suggests that some ecological aspect of this particular coastal habitat is determining the current distribution of the white morph, and thus that natural selection is involved.

Similar dark/pale colour polymorphisms are also found in non-avian vertebrates. Again, ecological components of this variation are generally not well known. A few have been linked to crypsis, such as in Deer mice *Peromyscus* (Linnen *et al.*, 2009) and in lizards (Rosenblum, 2006). A particularly intriguing parallel might be found in the white Kermode or 'Spirit' bear of coastal British Columbia. This white morph of the Black bear *Ursus americanus* is caused by a single mutation and is rare (200–300 individuals globally). It reaches frequencies of up to 50% on some isolated coastal islands (Ritland *et al.*, 2001). Coastal Black bears depend for much of their protein on salmon fishing. White bears have a higher hunting success because they are (as experimentally confirmed) less visible against a bright sky. As a result, white bears have a more marine stable isotope signature than normal black bears (Klinka and Reimchen, 2009), and presumably a selective advantage over black bears. Hence, like the caracaras this leucistic population of bears is also geographically restricted and associated with a particular coastal habitat, and natural selection seems to favour white bears there.

Therefore, one possibility is that the white morph caracara is somehow better able to utilize the rich seabird colonies and other marine life as a food resource than dark caracaras. Maybe they are cryptic against rocks coated in bird excrements. Or maybe they resemble locally common pale-plumaged seabirds such as gulls, terns, and sheathbills. A thermoregulatory function (Roulin, 2004) is not likely, given that normal-coloured caracaras are found from subantarctic to tropical climates without any geographic variation in plumage colour (Dove and Banks, 1999). Another possibility is that the allele that determines melanin production

has pleiotropic effect(s) on other physiological or behavioural processes (reviewed in Ducrest *et al.*, 2008). This could create a genotype × environment interaction in fitness: perhaps lacking melanin makes white morphs fitter in their coastal habitats for reasons unrelated to their actual colour. Note that this explanation still invokes natural selection to locally maintain leucism.

In conclusion, we infer that leucism in our population of coastal caracaras has a genetic basis, most likely caused by a mutation at a single locus. This is in line with the majority of other studies on leucism (Harrison, 1985). We further refute the possibility that inbreeding and genetic drift explain the high frequency of leucistic individuals in our population. Instead, all data point towards a selective advantage of leucistic individuals in their particular type of habitat. As such, this study provides an example that selection can maintain geographical variation in colour in birds.

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